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The genera of the fern tribe Vittarieae: their external morphology, venation, and relationships

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(WITH PLATES 2–8)

The fern tribe Vittarieae comprises upwards of one hundred species of simple-leaved tropical epiphytic ferns divided among six genera. The tribe is of particular interest because it includes in one of its genera, *Monogramma* Schk., two species which in leaf and stem structure stand at the bottom of the scale of vascular plants. In these species the leaf is a tiny threadlike structure with a single vascular bundle throughout its length. The stem has a central strand of xylem a few cells thick. The sporangia are borne along one margin in a deep groove. It is hardly possible to imagine a simpler type of fern.

The tribe, however, forms a connected series arranged upon the basis of venation pattern, beginning with *Monogramma* and ending, in the most advanced genera, in a well-developed reticulate scheme. The species of the intermediate genera furnish all the intermediate steps between the two extremes. Furthermore, in the ontogeny of the more advanced genera the same series of venation patterns is repeated, affording a double chain of evidence by which the origin of this reticulate type can be traced. The stele varies from a tiny protostele in some of the species of *Monogramma* to an advanced type of siphonostele in *Anetium* et al.

The tribe offers therefore an exceptionally good field for studies in comparative morphology and has also added interest due to

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the fact that the field is almost entirely unworked, except from a purely descriptive standpoint. Luerssen has described the sporangial groove in the genus *Vittaria;* Mettenius has figured a leaf section of a species of the same genus; E. C. Jeffrey, and E. G. Britton and A. Taylor have described and figured the leaf and stem structures of single species, also of *Vittaria*. Goebel has described the gametophytes of species in several of the genera and E. G. Britton and A. Taylor described the same stage in another species. There is, however, no occasion for considering these scattered papers except as of interest in connection with the detailed study.

The present paper deals almost entirely with the comparative external morphology and venation of the genera and the probable relationships indicated by these characters. The data needed in this connection, as well as for the internal morphology on which it is intended to publish later, were obtained in the course of a taxonomic study of the species. The taxonomic problem is in many respects the most difficult of all, as the species are often very similar externally and require microscopic study, as in *Isoetes*. The species groups will be revised from time to time as soon as sufficiently understood. Many of the necessary data for such revisions are now at hand.

The material studied has been almost entirely in the form of dried herbarium specimens. Usually it has been possible to soak these and get fair sections when necessary, although in the case of poorly dried plants soaking does not produce the desired results. The work has been carried on during the last five years at the New York Botanical Garden, and mainly with the material in the Underwood Fern Herbarium at that place. Besides this material I have had also loans from the herbarium of the Botanisk Museum at Copenhagen, the Eaton Herbarium at Yale University, the National Herbarium at Washington, the herbarium of the Bureau of Science at Manila, and from Dr. E. B. Copeland's private herbarium of Philippine ferns. I am grateful to those to whom I owe the privilege of examining the material in these herbaria, to Dr. N. L. Britton of the New York Botanical Garden, to Mr. Carl Christensen of the Botanisk Museum of Copenhagen, to Professor A. W. Evans of Yale University, to Mr. W. R. Maxon of the U.

S. National Museum, to Mr. E. D. Merrill of the Bureau of Science, at Manila, and to Dr. E. B. Copeland of the College of Agriculture of the University of the Philippines. I am also indebted to Dr. H. Christ of Basel for several favors in the way of loans of material, and to Prince Roland Bonaparte of Paris for a specimen and photographs of the type material of *Hecistopteris Werckleana* Christ.

Opportunity has been had to observe living material of several species grown in the conservatory of the New York Botanical Garden. Lastly I have had formalin and alcoholic material of a few species, collected in the field through the kindness of Mr. R. S. Williams of the New York Botanical Garden, and of Mr. E. D. Merrill and Dr. C. B. Robinson of the Bureau of Science at Manila.

Professor Carlton C. Curtis of Columbia University, and Dr. Marshall A. Howe of the New York Botanical Garden have aided me by reading manuscript and my thanks are due them for their help.

In the succeeding pages, the matter is presented under the following headings:

I. Tribal characters.
II. Genera.
III. Ontogenetic stages.
IV. General considerations.
Summary.
Plates.

I. TRIBAL CHARACTERS

(PLATE 2, etc.)

Reference has already been made in a general way to some of the tribal characters of the Vittarieae. These must now be set down in detail before any comparative study of the genera will be profitable. It should be noted that the tribe is to be distinguished from others by no one of the characters alone, the specialized epidermal idioblasts alone perhaps excepted, but depends rather for its separation upon the agreement which the included species show as regards several characters.

Plants comparatively small, essentially epiphytic, i. e., on trees, mossy rocks or logs, rarely on the ground, herbaceous, both as to stems and leaves, never with any sclerenchymatous tissue, the mechanical tissue being in the form of collenchyma.

Stems creeping, covered with clathrate scales.

Leaves simple, entire (*Hecistopteris* excepted), the venation when divided at all, anastomosing (*Hecistopteris* excepted) to form simple areolae without included veinlets.

Sporangia borne in lines of indefinite extent along the backs of some or all of the veinlets (*Anetium* excepted), often forming branching series, sometimes anastomosing, superficial in a few species but usually immersed in the leaf substance in distinct grooves. Epidermis usually provided with specialized cells, the outer walls of which are very greatly thickened.

These characters, with the exceptions noted, hold true for all the species. In habitat the species are all essentially alike, except that one species, *Antrophyum latifolium*, has been recorded by Dr. E. B. Copeland as occurring on the soil. Mr. R. S. Williams, who has collected a considerable number of the species, in the Philippines and in Central and South America, tells me he has often found the plants much wilted in the heat of the day but apparently not injured on this account. Some of them, at least, may often occur in exposed situations, and are probably essentially xerophytic. This may appear in the leaf structure. Thus, in *Vittaria lineata*, the leaf may have the epidermis reinforced by several tiers of thick-walled cells without chlorophyl, presumably to aid in conserving the water supply. This, the commonest American species of the tribe, occurs in exposed situations, epiphytic usually on palms.

The herbaceous character is a uniform feature. In Diel's treatment of the tribe, as presented in Engler and Prantl, Die Natürlichen Pflanzenfamilien, several species of an essentially woody nature are included, and these in the simplest and most tenuous of all the genera, *Monogramma*. These woody plants are mostly American species, which Dr. H. Christ has better separated as a distinct genus, following Presl, i. e., *Pleurogramma* Presl. There is ample evidence to show that they are not only not to be included in *Monogramma*, but that they may not even be retained in the tribe Vittarieae. They are hard, tough little plants with a strong development of sclerenchyma fibers in the

stem and leaves, and as another distinguishing feature, possess a dictyostele, a more advanced type of stele than occurs in the most specialized of the true Vittarieae. As a further proof of their proper differentiation it may be mentioned that they are connected through a series of species with *Polypodium* of the group including *P. serrulatum* and *P. marginellum*, with which they agree in stem, scale, and spore characters, not to mention others.

The clathrate scales are distinctive. (See PLATE 2, FIG. 9–11, 17.) In these only the internal walls are thickened, the result being a latticelike appearance, whence the name "clathrate." The superficial walls remain, but so thin and colorless as often scarcely to be apparent. In the majority of fern scales, the thickening is more even, and the scale usually appears concolorous and more or less opaque.

The outline of the leaves, that is, simple and entire, is to be correlated with the venation, which, except in the three or four smallest species, is always simply reticulate. The reticulation is based in most cases either on the plan of a midvein with uniform lateral areolae (PLATE 2, FIG. 1, 3), or the midvein may be lacking, and then all the veins are uniform (PLATE 2, FIG. 6; PLATE 6, FIG. 2). Consequently there are no predominating vein branches, and therefore no divisions of the leaf. It will be shown later that this areolate type of venation is derived from a free dichotomously divided type. The only exception to the rule of entire leaves, *Hecistopteris*, belongs near the bottom of the scale, and may be considered to have remained stationary in the dichotomously free-veined stage which appears in the ontogeny of several species of which the early stages have been studied. The different venation patterns above *Hecistopteris* depend upon the presence or absence of a midvein and the number of rows of areolae.

The soriation varies with the venation but is essentially of one type for all the species but one, *Anetium citrifolium*, and in this the aberrant type is found to have been derived from the usual plan. This statement may appear at first sight entirely unwarranted, but a survey of the whole tribe will show that the sporangia, with the one exception noted, are borne in lines usually of considerable but indeterminate extent along series of interlocking veinlets. In the simpler, narrowest-leaved genera, the lines

are necessarily unbranched, as in *Monogramma* (PLATE 3, FIG. 3, 8, 11) and *Vittaria* (PLATE 2, FIG. 4, 5), but in the genera with pluriseriate areolation the sporangial lines frequently fork, and in some species anastomose again. *Ananthacorus* is exceptional with its pluriseriate venation and two simple sporangial lines, one along each margin. *Anetium* has appeared even more exceptional as its sporangia have always been described as occurring in round sori and only over the intra-areolar tissue, but, as will be described in connection with the genus, the sporangia are sometimes along the veins even in this genus.

As noted in the tribal description, the sporangia in all but a few species are developed in grooves in the leaf tissue. Sometimes the margins of these grooves are extended to meet and form an indusiumlike protection. This is especially well shown in species of *Monogramma* (PLATE 3, FIG. 2, 7, 9, 15, 16, 17) and *Vittaria* (PLATE 5, FIG. 6, 8, 9). Usually also, there are associated with the sporangia, and of coordinate origin, numerous paraphyses which develop before the sporangia, and probably serve, as Dr. Copeland has suggested, to protect these in their developmental stages. The sporangia are superficial in about ten species, and the paraphyses are wanting in about the same number, but only in part the same species.

The differentiated unequally thickened epidermal cells, the so-called "spicular" cells (PLATE 2, FIG. 7, 8), are said by Goebel to occur only in the Vittarieae. Copeland has recorded their absence in a species of *Antrophyum*. I have not examined the species carefully as to their presence, but have noted them frequently. Goebel, Mettenius, and Luerssen found them present in the several species they studied.

II. GENERA

The species of the Vittarieae seem to fall naturally into seven generic groups. According to the usual taxonomic treatments there are only six, but one of these seems better divided into two. The characters upon which the genera are to be separated are mainly those of venation, but the arrangement of the sporangia is also used in the case of three genera. Of the seven genera here

recognized, three show very simple venation patterns. Thus, *Monogramma* has either a single veinlet in the leaf or at most one, two, or three divisions of the trace forming as many areolae. In *Hecistopteris* the venation consists of a few free veinlets formed by the dichotomy of a single bundle at the base of the leaf. In *Vittaria* the venation consists of a midvein with a single row of simple areolae along each side. The number of the areolae in each row may be as few as one, or there may be very many, but the pattern is always simple.

In the other four genera, *Anetium*, *Ananthacorus*, *Antrophyum*, and *Polytaenium*, as here described, there are always more than two rows of areolae across the leaf, so that the name "pluriseriate" may be applied to this type of venation. For want of a better term the three genera named in the preceding paragraph may be designated the "simpler genera."

The generic characters may be briefly contrasted as in the following taxonomic key:

Veins free-forking. 2. *Hecistopteris.*
Veins, if more than one, anastomosing to form simple areolae.
  Sporangia in a single marginal or dorsal line. 1. *Monogramma.*
  Sporangia in two or more lines or in small groups.
    Venation consisting of a midvein with a row of areolae along each side. 3. *Vittaria.*
    Venation of more than two rows of areolae across the leaf.
      A percurrent midvein present, the lateral veins smaller and secondary.
        Sporangia in two submarginal rows along the outermost veinlets. 5. *Ananthacorus.*
        Sporangia usually in more than two lines, but never only on the outermost veinlets. 4. *Polytaenium.*
        Sporangia usually in small groups or patches on the intra-areolar spaces. 6. *Anetium.*
      No percurrent primary midvein. 7. *Antrophyum.*

A. SIMPLER GENERA

1. MONOGRAMMA Schkuhr, Crypt. Gewächse 1: 82. *pl. 87.* 1809

Type species, *Pteris graminea* Poir. Type specimen from the Bourbon Islands, *Roemer.*

The genus *Monogramma*, properly delimited, that is, with the polypodioid American species excluded, includes five species, all

native in the Old World tropics. Among these five species are two that show the simplest leaf structure known among vascular plants. In these the leaf has only a single simple vein (PLATE 3, FIG. 1, 20) and in one of these two species the whole leaf is only 2–2.5 cm. long, and scarcely 1 mm. wide. In the other three species, the leaf trace may divide once or twice to form one or two areolae, but even in these species, the leaves are very tenuous (PLATE 3, FIG. 6, 10, 12, 13).

In characters other than those of venation, the species all agree with the tribal description given. The scales are clathrate; spicular cells have been recorded, although not all the species have been examined as to this character; and the sporangia are in indeterminate lines along the vein or veins and are protected by being depressed in the leaf tissue. Mixed with the sporangia are paraphyses of the type common for the tribe. As it happens, these take two forms in *Monogramma*. In three of the species, viz., in *M. paradoxa*, *M. subfalcata*, and *M. trichoidea*, occurs what is probably the simplest type of paraphysis in the tribe. The end cell, which in other species is usually capitate and strongly colored, or otherwise differentiated, is in these three species merely rounded off, and hyaline like its stalk cells. The whole structure is often hard to distinguish from the pedicels of the sporangia (PLATE 3, FIG. 16, 18).

In the other two species, *M. graminea* and *M. dareicarpa*, the paraphyses have strongly colored and capitate end cells, which collapse in a characteristic way when dried, the end becoming depressed so that the end cell then appears like a small bell (PLATE 3, FIG. 4, 5). Paraphyses of this type are also found in *Hecistopteris* and in one group of *Vittaria*.

The spores were seen for all the species but *Monogramma subfalcata*, and are of the triplanate type, and like those of this type in the other genera of the tribe.

Because of the interest which may attach to these simplest of all ferns, and the need of exact determinations, a brief descriptive key is offered. All the species have been adequately differentiated by figure and description but only in separate places. There are good figures of the gross leaf anatomy of four of the five species, but for comparison with each other and with the

species of the other genera of the tribe, all five are here shown together in one plate (PLATE 3). The species may be compared as follows:

Leaf trace undivided throughout, paraphyses distinctly capitate.
Leaves 5–10 cm. long (Mauritius). *M. graminea.*
Leaves not more than 3 cm. long (Borneo, Philippine Is.). *M. dareicarpa.*
Leaf trace with 1–2 or rarely 3 divisions, paraphyses not capitate.
Leaves hairlike; twisted, with sporangia in 1–3 separated grooves in a line along the leaf (Philippine Is.). *M. trichoidea.*
Leaves flat, more or less falcate, the sporangia in a single or in two parallel grooves.
Leaves about 2.5 cm. long, with only one areola and soral line (New Hebrides). *M. subfalcata.*
Leaves much longer, up to 25 cm. long, often with two areolae and soral grooves (Oceanica and Malaysia). *M. paradoxa.*

The structure of the leaves and their venation is sufficiently well shown so that little description is needed. In *M. paradoxa* the majority of the leaves show only a single areola and sporangial line, but the type with two, as figured, is not unusual. In *M. trichoidea* the section shows that the leaf trace may divide, at least along some of the soral grooves, but the material does not soak up well and it was not determined whether this is true in all cases. The shape of the sporangial groove appears from the gross study of a number of leaves to vary somewhat, being often more nearly equal-lipped. *M. graminea* and *M. dareicarpa* are alike in the type of soral groove. There is possibly a slight difference in the shape of the paraphyses. This, together with the difference in size and the wide separation in range, makes adequate specific separation. *M. subfalcata* is similarly related to *M. paradoxa*, and is not so well separated in distribution, but from the material studied, and this included a considerable series of *M. paradoxa*, their separation appears justified.

From the standpoint of species differentiation, *Monogramma* is interesting as showing the possibilities of variation in the very simple structure involved. The genus stands at the bottom of the scale in comparison with other vascular plants, the mature leaf being simpler in structure than the stage which appears in the first leaf in other ferns. The differentiation is, as noted, usually coupled with differences in the distribution, but at least three of the species may occur in the same general region.

The generic separation of *Monogramma*, as compared with the simpler species of *Vittaria*, depends on the simplicity of the venation and the simple sporangial line. In *M. graminea*, *M. trichoidea*, and *M. dareicarpa*, the line is lateral, as shown in the plate. In the other two species it is dorsal, but even in the two-areolate leaves of *M. paradoxa*, the two grooves open together along the midvein and at maturity form but a single line of sporangia. But between this type and the type characteristic of *Vittaria* there is really no very wide "generic" distinction.

2. HECISTOPTERIS J. Smith, London Jour. Bot. 1: 193. 1842

Type species, *Grammitis pumila* A. Spreng. Syst. Suppl. 31. 1828. (Type locality, "Ad corticem arborum, in Surinam. —Weigelt.")

Hecistopteris is commonly recognized as including a single epiphytic species, *H. pumila* (A. Spreng.) J. Sm., native in northern South America. Excluding the simple-veined species of *Monogramma*, *Hecistopteris pumila* is the only free-veined species in the whole tribe of the Vittarieae. It is, like *Monogramma*, of particular morphological interest because of the very primitive character of its venation, both as compared with the more highly developed genera of the Vittarieae and as regards ferns in general. Probably all ferns in whatsoever family, *Monogramma* alone excepted, exhibit in their very early ontogeny a stage of development in which their venation corresponds to the type characteristic of mature *Hecistopteris*.

As noted above, only one species is commonly recognized. Dr. Christ has given subspecific names to three variant forms but without urging their recognition as species. The original figure shows plants similar to that illustrated in FIG. 12–16 of PLATE 4. FIG. 1–8 and 19–22 of the same plate are taken from plants of two Bolivian collections and appear to represent a rather distinctive development, approaching in some respects to the outline and venation of the larger species of *Monogramma*. Such a form is perhaps worthy of further study with a view to determine whether the form differences are not correlated with distinctive distribution.

The stem is very slender and dorsiventral in structure. Only herbarium material has been obtainable for study and it has not been possible to obtain any of this which would soak up well enough to allow a good section to be made. The thickness of the stems, not greater than that of the simpler species of *Monogramma*, would indicate that the internal structure must be very simple and deserving of thorough morphological investigation.

The leaves as figured (PLATE 4) are sufficiently described as to venation, this being merely free and dichotomous. As to soriation, apparently any of the ultimate and next larger veins may bear sporangia. These are borne quite superficially, an unusual feature in this tribe. The only protection to the sporangia is afforded by the paraphyses, assuming that these develop earlier than the sporangia, as is true in all the species of the tribe in which their development has been noted. In this way the young sporangia would be partially protected during the earlier part of their development.

The paraphyses are of the type already described for *Monogramma graminea* and *M. dareicarpa*, and further, they are practically identical with those characteristic of *Vittaria* of the group of *V. remota* Fée. The spores are diplanate, another point of similarity with the *V. remota* group. The scales are of the usual clathrate type.

Goebel, by his study of the gametophyte of *Hecistopteris*, first succeeded in convincing botanists that this genus is properly to be associated with *Monogramma* and *Vittaria* rather than included as a species of the "catch-all" genus *Gymnogramma* as interpreted by earlier writers. John Smith, however, had already pointed out clearly, in connection with his original description of the genus, that it is "only distinguished from that genus [*Monogramma*] by the cuneiform, usually laciniate character of its fronds, and consequent forked venation." His statement would have been more accurate if he had partly reversed the order of the words and made the outline of the "fronds" the consequence of the forked venation.

The taxonomic separation of *Hecistopteris* is simple by reason of its free-forking venation. As a matter of fact, however, its actual phylogenetic separation from the simpler species of *Vittaria*, especially of the *V. remota* group, is probably not very great.

Notice should be taken here of two other names recently proposed in *Hecistopteris*, viz., *Hecistopteris Werckleana* Christ (Bull. Herb. Boiss. II. **7**: 265. 1907), and *H. minima* (Baker) Benedict (Bull. Torrey Club **34**: 457. 19 O 1907). The latter is the earlier species and was originally described by Baker as *Antrophyum minimum* and so appears in Christensen's Index Filicum. Dr. Christ's species *Werckleana* was also originally described as an *Antrophyum*, but was soon after shifted by him into *Hecistopteris* on account of the occasional forking of the tips of the leaves. This, however, is merely the abnormal forking frequent in all species of ferns. As it turns out, *Antrophyum Werckleanum* is identical with *A. minimum* Baker. This I have been able to determine through the kindness of Prince Roland Bonaparte, from whose herbarium a plant of the original collection of *Werckleana* has been obtained (PLATE 2, FIG. 4. Compare with FIG. 5 of the same plate, drawn from type material of *H. minima*). Both have the venation of *Vittaria*, and the species, which will need to be known under Baker's name, should henceforth be called **Vittaria minima** (Baker) Benedict comb. nov. (PLATE 2, FIG. 4, 5). *Antrophyum minimum* Baker, Ann. Bot. **5**: 448. 1891.

Hecistopteris minima Benedict, Bull. Torrey Club **34**: 457. 19 O 1907.

Antrophyum Werckleanum Christ, Bull. Herb. Boiss. II. **5**: 11. 1905.

Hecistopteris Werckleana Christ, Bull. Herb. Boiss. II. **7**: 265. 1907.

3. VITTARIA J. E. Smith, Mem. Acad. Turin. **5**: 413. *pl. 9.* 1793

Type species, *Pteris lineata* L. (Type specimen from Santo Domingo.)

The genus *Vittaria* shows in its simplest species, *V. sikkimensis* Kuhn, a venation similar to that of *Monogramma paradoxa*. (Compare PLATE 3, FIG. 13, and PLATE 5, FIG. 18, 20, respectively.) It differs even in this species in having two separate sporangial grooves, and this character furnishes the most obvious generic mark. The venation consists always of a median vein with a row of areolae (1–many) along each side. This venation may be characterized as biseriate.

Vittaria includes probably at least forty species and is the largest genus of the tribe. More than half of these are native in the Old World tropics, and of these I am unable to give the exact number, owing to insufficient material of all except the Philippine species. Christensen in his Index recognizes forty-six species, of which fifteen are American. Several of these may be reduced to synonymy or referred to other genera, but there appear to be several undescribed and some others listed as synonyms which should be recognized, so that the number of species to be recognized will remain about the same.

According to the tribal description, species of a woody texture, with sclerenchymatous tissue, and with dictyostelic vascular systems, must be excluded from *Vittaria*. This will reduce Christensen's list of Old World species by two or three names, such as *V. minor* and *V. pusilla*. Dr. Christ puts these species in *Pleurogramma*, and there appears to be a close relation to this group, but the venation is somewhat different from that in the American species, in which it consists of a midvein with free pinnate veinlets. In the so-called Old World Pleurogrammas, the lateral veinlets form two rows of areolae, which, however, have free outer veinlets. Like all other groups of the tribe Polypodieae, these two stand much in need of a realignment.

The characteristic venation of *Vittaria* is well shown in the figures of *V. minima* in PLATE 2, FIG. 4 and 5. All the various modifications shown in PLATE 5 are easily reducible to this simple pattern. The greatest differentiation that takes place has to do with the direction in which the areolae are elongated; if in a line parallel to the midvein, the type shown in PLATE 5, FIG. 1, results. This is characteristic of all the very narrow species like *V. lineata* and others, including a majority of the species in the genus. The species of this type figured, *V. intramarginalis*, does not begin to show the extent to which this leaf elongation may be carried. Leaves of *V. lineata*, not more than three or four millimeters in breadth, reach a length of one thousand millimeters. The veinlets in such cases are much farther apart than indicated in the figure of *V. intramarginalis*. In the other type, the areolae are elongated in lines parallel to the first direction of the veinlets, that is oblique to the midvein. This results in much broader leaves, as shown in FIG. 7, 10, and 11 of PLATE 5.

These variations in venation are not accompanied by any features which would indicate that there is any tendency to subgeneric grouping on this basis. In fact there are all intergradations between the extremes of both types; the two forms occur in both the eastern and western hemispheres, and, moreover, in both the natural subgenera into which *Vittaria* may be divided.

These may be differentiated as follows:

EUVITTARIA. [Type species, *V. lineata* (L.) J. E. Smith.]

Stem dorsiventral, phyllotaxy distichous, leaf trace double in all but a few simple species, stem and petioles pale. Spores diplanate or triplanate, paraphyses variable.

Includes most of the species, all the Old World species, and more than half those native in America.

Radiovittaria subgen. nov. (Type species, *V. remota* Fée.)

Stem radial, phyllotaxy polystichous, leaf trace always single, stem and petioles brown, owing to the highly developed collenchymatous strengthening tissue. Spores diplanate, paraphyses always of the *Monogramma graminea* type (PLATE 2, FIG. 18–20).

Includes *V. remota* Fée, *V. Gardneriana* Fée, *V. minima* (Baker) Benedict, *V. stipitata* Kunze, and *V. Orbignyana* Fée; also two Bolivian species not yet described.

These two subgenera show points of difference often considered as of generic value but the venation and soriation are alike in both, and the needs of descriptive taxonomy are probably better served by retaining both groups under the one generic name *Vittaria*.

The stem externally appears about the same in all species of *Vittaria*. In some of the Old World species the internodes are of considerable length, but in most of the species the leaves are close together. The difference noted as to the color of the *Radiovittaria* stem is not apparent until the scales are removed. The scales are essentially the same in all the species, the only variation being in size and amount of thickening in the internal walls. (See PLATE 2, FIG. 9–11, 17.) Also in some species these walls may show granular or papillose markings. The spores, as already noted, are either diplanate or triplanate. The paraphyses show a number of different forms, which are of considerable value in grouping the

species for identification but which need not be described here. They consist, as noted in the tribal descriptions, of enlarged, usually brown or yellow end cells, borne on single or branching multicellular pedicels and associated with the sporangia.

The sporangia are always borne along the outer interlocking portions of the veinlets as continuous lines along the greater part of the lamina (PLATE 2, FIG. 4, 5). With perhaps not more than two exceptions, the sporangial line is always in a groove or depression of greater or less extent. FIGURE 12 of PLATE 5 shows a very slightly depressed groove. FIGURES 6, 8, 9, and 21 of the same plate show some of the deeply grooved species and the variety of ways in which the groove may be disposed. According to the development of the grooves, the species have sometimes been described as possessing indusia or otherwise. FIGURES 6 and 12, respectively, illustrate these two types. The use of this term is hardly advisable as there is no real differentiation of one lip as a distinct indusium. This is equally true of *Monogramma* (PLATE 3, FIG. 2, 7, 9, 14, 15, 19), as also of all the species in which the receptacle is sunk in a groove.

The various types of sporangial groove have been thoroughly studied and figured by Luerssen. (Filices Graeffeanae, in Schenk and Luerssen, Mitt. Gesammt. Bot. 1: 57. *pl. 11, 12.* 1871.) This, by the way, is the only feature of the Vittarieae that has been adequately studied through any considerable number of species.

It has already been noted that the venation of the simplest species of *Vittaria* is essentially the same as that of *Monogramma paradoxa*, and that the separation in this direction must depend on the separate sporangial lines. With respect to the more advanced genera, the characters of the venation furnish the best distinction. As regards the soriation, certain species of the more advanced genera appear sometimes like *Vittaria*.

B. PLURISERIATE GENERA

The remaining genera of the tribe all show a more advanced type of venation than that of *Vittaria*. If the latter with its two separate rows of areolae may be called "biseriate," the more complex type may well be named "pluriseriate," since there are

always more than two rows of areolae. Of this pluriseriate type two distinct patterns occur in the tribe, the distinction depending upon the presence or absence of a midrib (PLATE 6, FIG. 1 and 2).

That this distinction is important is evidenced by the distribution of the species. All the American species possess a distinct primary vascular strand, a complete midrib, in relation to which the areolation is secondary and derivative. In the Old World species, on the contrary, there is no complete primary axial vein. There occurs in some few species of this region an incomplete midrib, but in none of these species is this midrib ever maintained as predominant throughout the leaf, and in all the Old World species the areolation is in part or entirely derived by the dichotomy of the several veins present at the lower part of the blade.

As further evidence of the fundamental character of this distinction in venation, shown in the mature sporophytes, the fact should be noted that among the American pluriseriate species three distinct genera, based on sporangial arrangement, are recognized; that is to say, subsequent to the separation of the continental groups on the basis of venation, one of these groups has been further differentiated into three well-marked genera. Surely continental venation differences in this case deserve precedence over intracontinental soral variations. Additional evidence is offered farther along in connection with the description of the ontogenetic stages.

Notwithstanding, however, this accepted generic separation within one venation group, the larger number of American pluriseriate species have been retained under the same generic name as the Old World species, viz., *Antrophyum* Kaulf. The principal reason for such retention under one name has been the fact that the soriation is somewhat similarly indefinite in both groups. But it should be apparent, I think, as expressed above, that as a generic character the venation pattern must take precedence over the sporangial arrangement, and that *Antrophyum* as at present delimited, includes two generic groups more distinct from each other than are the three pluriseriate groups which are now kept apart because of different sporangial arrangement.

For this reason the American species formerly classified under the name *Antrophyum* are here included under a different name,

Polytaenium Desv., and a revised description is given with *P. lineatum* (Sw.) Kaulf. as the type species. *Antrophyum* proper is typified by an Old World species, *A. reticulatum* (Forst.) Kaulf. The distinguishing feature of *Polytaenium*, the double or "twin-net" type of venation as compared with the single net type of *Antrophyum* is shown typically in PLATE 6, FIG. 1.

4. POLYTAENIUM Desvaux*

Type species, *Hemionitis lineata* Sw. (Type specimen from Jamaica.)

Herbaceous epiphytic ferns with creeping dorsiventral rootstocks and fasciculate, simple, entire leaves, the phyllotaxy distichous; scales of the rootstock and leaf bases clathrate.

Leaves glabrous except for a few scales at the base, linear to broadly oblanceolate, long-decurrent below; leaf trace double, the bundles uniting in the leaf base to form the primary midvein, from which branch secondary veinlets to form two or more rows of simple areolae along each side.

Sporangia along the veinlets and sometimes along the midvein in lines of indefinite extent, often branching, sometimes reticulate, usually immersed in slight grooves; paraphyses absent; spores triplanate (except in one species).

During the nearly four years since my first paper dealing with the species of *Polytaenium* was published, I have had occasion to examine from time to time newly collected herbarium material. More recently I have been studying the internal stem characters and have made sections of the leaves in order to gain a better understanding of their characters. This study has in general

*Under the title The Genus *Antrophyum*—I. Synopsis of the subgenera and the American species (Bull. Torrey Club **34**: 445–458. 19 O 1907), I have already given a taxonomic treatment of the species to be included in *Polytaenium*. At that time, basing my descriptions on a careful external study of the plants, I recognized nine species. Eight of these should now be named anew as follows: (combinationes novae) **Polytaenium cayennense** (Desv.), *Hemionitis cayennensis* Desv. Berl. Mag. **5**: 311. 1811; **Polytaenium lanceolatum** (L.), *Hemionitis lanceolata* L. Sp. Pl. 1077. 1753; **Polytaenium brasilianum** (Desv.), *Hemionitis brasiliana* Desv. Prod. 216. 1827; **Polytaenium discoideum** (Kunze), *Antrophyum discoideum* Kunze, Bot. Zeit. **6**: 702. 1848; **Polytaenium anetioides** (Christ), *Antrophyum anetioides* Christ, Bull. Herb. Boiss. II. **5**: 12. 1905; **Polytaenium Dussianum** (Benedict), *Antrophyum Dussianum* Benedict, Bull. Torrey Club **34**: 453. 19 O 1907; **Polytaenium Jenmani** (Benedict), *Antrophyum Jenmani* Benedict, Bull. Torrey Club **34**: 454. 19 O 1907; **Polytaenium ensiforme** (Hook.), *Antrophyum ensiforme* Hook. in Benth. Pl. Hartweg 73. 1841.

confirmed the results of the early external study and has also added some valuable facts to aid in species differentiation.

One result of this further study has been the discovery of an undescribed species, which by reason of its venation and sporangial arrangement, serves as a connecting link with *Vittaria* and therefore deserves a name and description in this place.

Polytaenium quadriseriatum sp. nov.

Rootstock creeping, dorsiventral, the scales clathrate; leaves fasciculate, in two rows, firmly herbaceous, the petiole 3-angled, the blade linear, 12–20 cm. long, 3–5 mm. broad, narrowed very gradually and equally both ways, the apex acute; venation consisting of a midvein with two rows of areolae along each side; sporangia in two long continuous deep grooves along the outer margins of the costal areolae, with sometimes additional short grooves along the outer areolae, the margins of the grooves produced so as to meet, covering the sporangia when young; spores triplanate, no paraphyses. (PLATE 7, FIG. 8–10.)

Type from Hayti, *Nash & Taylor 1360*, in Underwood Fern Herbarium, N. Y. Botanical Garden.

The material on which this species is based was originally identified as *Vittaria intramarginalis* and was discovered during a study of that species. At first this identification was maintained and the specimen was looked upon as an aberrant *Vittaria*, but further study has made it evident that it should not be retained in that genus and species, but is rather more nearly related to *Polytaenium lineatum*. It differs from the *Vittaria* in the 3-angled stipe, and in color, texture, venation, and soriation. It resembles *P. lineatum* in these respects, but differs from this species markedly in size and general appearance. If comparison is made between FIGURES 3 and 8 of PLATE 7, *P. quadriseriatum* will appear like *P. lanceolatum* in venation, but the soriation as figured for the latter species (FIG. 4) is entirely distinctive. *P. quadriseriatum* is particularly interesting, however, because of its position intermediate between the several species and two genera.

Question may be raised as to the necessity of two genera since there are connecting species. This does not seem an adequate objection, in view of the wide difference between the two types, as shown in most species, and since *Vittaria* in its special line of

development, generally shows as wide a divergence from the simple type as do the species of *Polytaenium*. Whatever its proper rank or name, the significance of *P. quadriseriatum* is the same, and it serves to connect the pluriseriate venation pattern of *Polytaenium*, *Ananthacorus*, and *Anetium* with that of *Vittaria*.

The venation of *Polytaenium* is illustrated by figures of several species (PLATE 6, FIG. 1; PLATE 7, FIG. 3–6, 8). By reference to these figures, it may be noted that the areolae decrease in size from the midvein toward the margin. In the narrow-leaved species, which have all the areolae parallel to the midvein, this decrease takes approximately the ratio of 1 : ½ : ¼, the length of a costal areola being taken as the unit. In the broader-leaved species, only the costal areolae are parallel to the midvein, and the divergence of the others increases their proportionate length, although a steady decrease in size toward the margin is still the rule. In the broadest species, *P. Jenmani*, as also in *Anetium*, the divergence in the outermost areolae approaches an angle of 90°. The other species furnish all gradations between this broadest type and that of the narrowest species, *P. quadriseriatum*.

The external stem characters are practically alike for all the genera, the only difference being in the size. The scales are of the general clathrate type and are alike except for some slight variations in size, shape, and margin. The spores are triplanate in nine out of the ten species here recognized, and these same nine species lack paraphyses.

One species, *Polytaenium ensiforme*, has both diplanate spores and capitate pyriform paraphyses. It was recognized in my earlier paper as a distinct subgenus, *Scoliosorus* Moore, but perhaps this distinction is unwarranted.

Another subgenus based on a soral difference, namely, *Polytaenium* Desv., was also recognized at that time, including a single species, "*Antrophyum*" *lineatum*. If this were worth maintaining, *Polytaenium quadriseriatum* would now have to be included, the two species together to constitute the subgenus *Eupolytaenium*, but there does not appear to be any necessity for such separation.

The sporangia are borne in lines of greater or less extent, in some species always simple, in others branching and, in still others incompletely anastomosing. In most of the species of *Polytaenium*

the lines are in slight grooves or even superficial. In the *P. lineatum* type the lines are much elongated, and, with rare exceptions, unconnected (PLATE 7, FIG. 8). In the pair of species which show this type, the sporangia are also developed in deep, partly covered grooves. In *P. lanceolatum*, a species which belongs next to *P. lineatum*, the sporangia are nearly superficial and in short, often more or less branching lines along the longitudinal veinlets (PLATE 7, FIG. 4). The specimens of *P. lanceolatum* figured are of the variety *Feei*. Typical *P. lanceolatum* is much longer and narrower in proportion, and shows soriation not so unlike *P. lineatum*, but as *P. quadriseriatum* and *P. lineatum* are situated near the border line between *Vittaria* and *Polytaenium*, it is not surprising that they should show a connecting type of soriation. In true Old World *Antrophyum*, all grades of soriation between a vittarioid type and the dichotomous type of *A. reticulatum* and *A. plantagineum* (PLATE 7, FIG. 11), and further a practically complete reticulation, as in *A. Boryanum*, may be found.

Polytaenium may be considered as a well-marked genus, notwithstanding its obvious origin from a form like *Vittaria*. The whole tribe shows evidence of being of recent origin, and if so, it is not strange that the connecting links between the genera have been maintained.

5. ANANTHACORUS Underwood & Maxon, Contr. U. S. Nat. Herb. **10**: 487. 1908. (PLATE 2, FIG. 2 and 3)

Type species, *Pteris angustifolia* L. (Type specimen from the West Indies.)

Ananthacorus includes a single species, *A. angustifolius*, which has been included during its existence in a large number of genera of varying affinities. Goebel pointed out its relationship to the Vittarieae on the basis of its spicular cells but did not give it a generic name. Several attempts have been made so to signalize it but they have failed by reason of nomenclatorial difficulties until the action was taken which gave it its present name. Christensen, following Diels, included it with *Vittaria* because of its two sporangial lines (PLATE 2, FIG. 3), but that location can scarcely be maintained. These two lines are not homologous with those of *Vittaria*. If they were, they would be located along the costal

areolae, for in the pluriseriate type of venation these are true homologues of the costal and only areolae in *Vittaria*. *Anantha-corus* might better be considered as included in *Polytaenium* rather than in *Vittaria*, but the definitely localized fruiting lines, which are never so definitely localized in *Polytaenium*, furnish adequate ground for generic separation.

The venation as figured (PLATE 2, FIG. 3) is of the ordinary pluriseriate type described for *Polytaenium*. The scales are clathrate. The sporangia are in shallow grooves (PLATE 2, FIG. 2). The spores are diplanate. Pyriform capitate paraphyses of an ordinary sort are present.

6. ANETIUM Splitgerber, Tijdschr. Nat. Gesch. 7: 395. 1840. (PLATE 2, FIG. 1)

Type species, *Acrostichum citrifolium* L. (Type specimen from Martinique.)

Anetium, with a single species, *A. citrifolium*, has long appeared an anomalous genus and its proper position as regards other ferns has been in question, but I think I have here sufficient evidence to locate it properly.

Its venation is of the *Polytaenium* type in its highest development and does not need further discussion, neither do its other characters of vestiture, spores, or epidermal cells, all of which agree with the general types characteristic of the tribe.

Only the arrangement of the sporangia has caused uncertainty as to its systematic position. The sporangia have always been described as occurring only over the parenchyma within the areolae, and this is certainly the ordinary position. This has naturally resulted in placing the genus with the Acrosticheae, in which such sporangial position is the rule. In the Underwood Fern Herbarium, however, is a specimen which shows the variation in soral position indicated in the figure (PLATE 2, FIG. 1). In the lower part of the leaf the sporangia are along the veinlets in rather complete reticulation. Farther up this passes over into the usual *Anetium* type, but this single specimen is enough to show that the *Anetium* type has probably been derived from the *Polytaenium* type and that *Anetium* may be definitely and properly located in the Vittarieae.

The stem is much more elongated than in any other member of the tribe, the leaves being far apart. Judging from the peculiar stele, *Anetium* represents the greatest degree of modification in the whole tribe.

7. ANTROPHYUM Kaulfuss, Enum. Fil. 197. 1824

Type species, *Hemionitis reticulata* Forst. (Type from Upolu.)

The genus *Antrophyum*, as properly limited to the Old World plants having pluriseriate venation, includes approximately twenty-five species. This number is in excess of that given by Christensen, but it was determined after a careful study of material which contained nearly all the species described, and the estimate is conservative rather than excessive. The genus includes all the Old World species of Vittarieae having more than two rows of areolae through the leaf.

The origin and arrangement of the areolae is, as noted under *Polytaenium*, quite different from the type characteristic of that genus. Instead of proceeding from the midvein at regular intervals, as in *Polytaenium*, they are all directed toward the base and arise by the dichotomy of basal veins. Moreover, even when compared with the narrow types of *Polytaenium*, there is a considerable difference shown. In *Antrophyum*, areolae laterally adjacent to each other usually are practically equal in origin and length. In *Polytaenium*, on the contrary, especially in the narrow species, the areolae of the second row are always much shorter than those of the first, and are plainly secondary and derivative when compared with the first (PLATE 7, FIG. 2).

This difference between *Antrophyum* and *Polytaenium* is well illustrated in PLATE 6, FIG. 1 and 2. In *Antrophyum plantagineum*, the areolae decrease in size from the base toward the apex; in *Polytaenium cayennense*, the decrease takes place from the midvein outward.

It has already been noted that some species of *Antrophyum* possess an incomplete axial vein. This is especially evident in *A. semicostatum*, in which the midvein or "costa" may extend upward through half or even somewhat more of the lamina, but this species does not, on this account, serve to connect the *Antrophyum* venation pattern with that of *Polytaenium*. The midvein

in *A. semicostatum* is rather a parallel development than an indication of direct relationship with *Polytaenium*. *A. semicostatum* is very clearly related to the other Antrophyums.

As far as the characters of the mature sporophyte are concerned, *Antrophyum* seems to resemble most certain of the more divided forms of *Hecistopteris*. (Compare PLATE 4, FIG. 4, 5, etc., with PLATE 2, FIG. 6.) The leaves of *Hecistopteris* here referred to, possess a type of venation which is easily comparable with that of *Antrophyum nanum* Fée, shown in the last figure.

It is this type of venation, i. e., that of *A. nanum*, which is found in more or less modified form in all the larger species of *Antrophyum*. It is a type that seems to be better adapted than the *Polytaenium* type to the development of broad-leaved species, as *Antrophyum* includes at least two forms with orbicular blades and several others approaching this shape. One other interesting consequence of this dichotomous venation is to be noted, i. e., the leaf blade in all but a few species is broadest above the middle. In *Polytaenium* the blades are usually parallel-sided or elliptic.

In the characters other than those of venation there is considerable variation in *Antrophyum*, and because of a conjunction of several of these variations in connection with geographic isolation, I have separated a group of three or four species as a distinct subgenus, *Antrophyopsis*, native in southern Africa and adjacent islands. The differences are stated below in connection with each character.

The soriation in *Antrophyum* proper is variable between the limits shown in FIG. 1 of PLATE 7, and FIG. 2 of PLATE 6, respectively; that is, the sporangia may be borne either in single lines of greater or less extent (PLATE 7, FIG. 1 and 7), or they may be in lines that branch considerably (PLATE 7, FIG. 11). Always in *Euantrophyum* they are sunk in grooves. In *Antrophyopsis*, on the contrary, the soral lines are practically completely reticulated, and are entirely superficial. The spores in *Euantrophyum* are triplanate. The spores in *Antrophyopsis* are diplanate. The paraphyses are clavate in *Antrophyopsis*. In *Euantrophyum* the paraphyses may be either clavate or filiform. The stipe scales are of course clathrate in both, but the scale ribs in *Euantrophyum* are smooth; in *Antrophyopsis* they are verrucose.

A small but marked difference in the venation emphasizes further the distinction between the two groups. In *Euantrophyum* the marginal veinlets are rarely if ever free, but rather as indicated in FIG. 2, PLATE 6. In *Antrophyopsis* the outermost veinlets are free quite to the margin, and the latter is always more or less thickened. It should be stated, however, that although *Antrophyopsis* is confined to African regions, *Euantrophyum* is also represented there by one species, *A. immersum* Hook., outside of the usual subgeneric range in Oceanica and Malaysia.

Further reference will be made to *Antrophyum* in connection with the ontogenetic studies.

III. ONTOGENETIC STAGES OF VITTARIEAE

I have endeavored to show in connection with a study of the mature sporophytes of the various vittarioid genera that these form together a complete series of connected venation types, beginning with *Monogramma* at the lower end of the series, and ending doubly, on the one hand with *Polytaenium*, *Anetium*, and *Ananthacorus*, and on the other hand with *Antrophyum*. The *Polytaenium* type is connected with *Monogramma* through *Vittaria*. The *Antrophyum* type, it was noted, may, according to resemblances afforded by various mature species, be derived directly from the *Hecistopteris* type without the intervention of vittarioid or twin net types. If I have presented the facts clearly, it has been made apparent that the tribe offers a completely connected series of venation patterns ranging from the uninervate *Monogramma* type to the well-developed areolate system in *Polytaenium* and the others.

This series is even more clearly demonstrated in the ontogenetic stages of certain species of the more advanced genera, and I wish now to point out in detail just how exactly the ontogenetic series agrees with the series shown by the mature plants.

I have been able to obtain young sporophytes of five species, viz., *Vittaria remota*, *V. intramarginalis*, *Polytaenium lanceolatum*, *Ananthacorus angustifolius*, and *Antrophyum reticulatum*. The *Vittaria remota* material was obtained from plants grown at the New York Botanical Garden from spores brought from Jamaica,

by accident, with a lot of filmy ferns. Plants were obtained in all stages of maturity, so that identification was easy. The plants of *Polytaenium lanceolatum* were grown from spores taken from herbarium material collected in Cuba by Mr. Norman Taylor. Planted a month or so after collection, they germinated rather slowly and remained in the prothallial stage for a couple of years before developing sporophytes. None of these were brought to maturity, so that absolutely certain identification is not practicable, but the spores were sown in sterilized soil, the prothallia showed the peculiarities of the tribe as described by Goebel and by Britton & Taylor, and their continuity for the two years and their final production of the young sporophytes figured is indubitable.

The young plants of the other three species were obtained from material collected in the field. The *Vittaria intramarginalis* material was found on an herbarium sheet showing all stages up to maturity. That of *Ananthacorus* was obtained in like manner but lacks the very young stages. The material of *Antrophyum* was collected for me by Dr. C. B. Robinson, together with mature fruiting plants of the same species. This also lacks the earliest stages. This collection included numerous young plants of some other net-veined fern, but the venation type was entirely distinct from that of *Antrophyum* and easily separable.

During the course of my work I made an attempt to grow plants of *Antrophyum reticulatum* from spores obtained from herbarium material sent me by Dr. E. B. Copeland, but the spores proved inviable after their weeks of passage from the Philippines to New York City.

My first clue to the possible significance of the ontogenetic stages was obtained from figures of young *Vittaria lineata* (L.) J. E. Sm., published by Mrs. Britton and Miss Taylor.* This species, as it appears, is similar in its young stages to *V. remota* figured here.

Before proceeding to take up the description of the young material of the five species just noted, I wish to recapitulate in detail the venation series observed in connection with the study

*Britton, E. G., & Taylor, A. Life history of *Vittaria lineata*. Mem. Torrey Club **7**: 185–211. *pl. 28*. 1902.

of the mature sporophytes, and designate, by the name of the species best representing it, each successive stage of the series. This will then serve as a basis for the comparison of the ontogeny of each species.

MONOGRAMMA DAREICARPA Hook. (PLATE 3, FIG. 1)

The adult series begins with *Monogramma dareicarpa*, the simplest species in the whole tribe, the venation of which is a simple vein through the middle of the leaf. *M. graminea* has the same type of venation but is a larger plant, so *M. dareicarpa* may better serve as a starting point.

MONOGRAMMA SUBFALCATA Hook. (PLATE 3, FIG. 6)

This species presents a second stage in the venation series. As will be shown later, it probably represents a simple dichotomy of the leaf trace, modified to form the areola so characteristic of the venation of the tribe. *M. trichoidea* seems to belong here, but its structure is somewhat in doubt. *M. paradoxa* shows both this type and that of the third and next stage of venation.

VITTARIA SIKKIMENSIS Kuhn (PLATE 5, FIG. 18–20)

In *V. sikkimensis*, the leaf trace commonly divides twice to form two areolae, that is, a median vein with two lateral veins which anastomose anteriorly. This is in essence the venation of the genus *Vittaria*, but the latter may be better typified by a somewhat more advanced species.

VITTARIA INTRAMARGINALIS Baker (PLATE 5, FIG. 1)

This same type of venation is presented in characteristic form by a smaller species, *V. minima*, but I have chosen *V. intramarginalis* because it furnishes such a good transition to the next higher type. Within *Vittaria* the two divergent venation patterns might well be designated the *V. remota* and the *V. lineata* types; these are, respectively, the type with divergent areolae (PLATE 5, FIG. 11; also FIG. 7 and 10), and that with longitudinal areolae (PLATE 5, FIG. 1).

POLYTAENIUM QUADRISERIATUM Benedict (PLATE 7, FIG. 8)

Polytaenium quadriseriatum resembles *Vittaria intramarginalis* even more closely than the venation patterns might indicate.

This is shown in the figures of the cross-sections of the leaf. (Compare PLATE 5, FIG. 6, with PLATE 7, FIG. 9, 10.)

POLYTAENIUM CAYENNENSE (Desv.) Benedict (PLATE 6, FIG. 1)

Polytaenium cayennense merely represents the twin net venation in its complete development. All stages between it and *Polytaenium quadriseriatum* are presented by other species of the genus (PLATE 7, FIG. 3–6), and the same type is characteristic of *Ananthacorus* (PLATE 2, FIG. 3) and *Anetium* (PLATE 2, FIG. 1).

The two remaining genera offer venation patterns which at first sight appear to find no place in the series just presented, but represent rather a divergent series. Their exact relationship can be best shown when the ontogenetic stages are taken up. Their types may be designated sufficiently by the generic names alone.

HECISTOPTERIS J. Smith (PLATE 4)

PLATE 4 includes so many divergent leaf forms that it might at first sight appear advisable to employ more than one type name to characterize the different developments. These, however, all depend merely on the number of divisions of the leaf trace and are not recognized as distinctive of species, so that the number of types would be a matter of arithmetic. The *Hecistopteris* type then may be considered as including all forms that show a free-veined dichotomy of the leaf trace. It should be noted in passing that such *Hecistopteris* leaves as are represented by FIGURES 19, 20, and 22, of PLATE 4 are exactly analogous, as to the stage of development, with the *Monogramma subfalcata* stage. Similarly, the *Vittaria sikkimensis* stage is well represented in *Hecistopteris* by FIGURES 2, 9, and 15 of PLATE 4.

ANTROPHYUM Kaulf.

The *Antrophyum* type of venation is essentially that of *Hecistopteris*, but with the veins anastomosing to form areolae. This can be easily understood by comparing the venation of *Antrophyum nanum* (PLATE 2, FIG. 6) with that of some of the larger *Hecistopteris* leaves (PLATE 4, FIG. 4). In the larger species of *Antrophyum* the contiguity of the numerous veins so modifies the scheme as to make the dichotomy hard to trace. This modifi-

cation is sometimes accompanied by a prolongation of the leaf trace to form a partial midvein, thus approaching the *Polytaenium* type.

The ontogenetic stages of the several species to be described may now be compared in detail with the series of stages derived from mature plants, which has just been outlined.

VITTARIA REMOTA Fée (PLATE 8, FIG. 12–19)

FIGURES 12 and 13 represent clearly the *Monogramma dareicarpa* stage (PLATE 3, FIG. 1). FIGURE 14 is just as clearly like *M. subfalcata* (PLATE 3, FIG. 6), and FIGURE 15 is the next stage, that of *Vittaria sikkimensis* (PLATE 5, FIG. 18–20). FIGURES 16, 18, and 19 show an easy transition to the typical development of *Vittaria* through the *V. intramarginalis* stage to the stage typical of *V. remota* and others. FIGURE 17 is an abnormality, and FIGURE 19 shows another abnormality in having three incomplete lateral veins.

VITTARIA INTRAMARGINALIS Baker (PLATE 8, FIG. 1–11)

Vittaria intramarginalis, like *V. remota*, also starts with the *Monogramma dareicarpa* stage and attains finally to a mature *Vittaria* type, but it shows several very interesting intermediate stages. FIGURES 3–5 are like the corresponding stages of *V. remota* (FIG. 14, 15), i. e., they show once and twice forked veins, but the branches do not anastomose, hence the stages are to be compared with *Hecistopteris* rather than with *Monogramma subfalcata* and *Vittaria sikkimensis*, respectively. (Compare PLATE 8, FIG. 3–6, with PLATE 4, FIG. 1, 21, 22; 2, 9, 15; 3, 5, 10, 18, 20). FIGURE 7 (PLATE 8) should be compared with FIGURE 5 of the same plate as showing how the free-veined *Hecistopteris* type may be modified to form the *Vittaria* type. FIGURES 8–10 are somewhat aberrant leaves representing intermediate stages between the leaf illustrated in FIGURE 7 and the mature *Vittaria* type as illustrated in FIGURE 11.

POLYTAENIUM LANCEOLATUM (L.) Kaulf. (PLATE 8, FIG. 29–40)

Polytaenium lanceolatum also starts with the uninervate *Monogramma dareicarpa* stage (FIG. 38–40). FIGURE 39 shows an

abnormality in the vein unrelated to the real branching plan. FIGURES 35–39 are apparently on the same plane, but it is very interesting to find in one species that both the free-veined (FIG. 35, 37) and the areolate (FIG. 36) types may occur. It probably indicates, as was suggested earlier, that in the ontogeny of the higher genera of the Vittarieae there is not much difference between the free-veined *Hecistopteris* and similar areolate stages.

In the higher stages, *Polytaenium lanceolatum* is significant as showing the very early predominance of an axial vein. FIGURES 33, 32, 31, and 30 show successive stages in the venation development. FIGURE 29 is abnormal. FIGURES 30 and 31 are essentially analogous to the *Vittaria intramarginalis* stage. No later stages were obtained for this species, but these are probably like those figured in connection with *Ananthacorus*.

ANANTHACORUS ANGUSTIFOLIUS (L.) Und. & Maxon (PLATE 8, FIG. 20–23)

The earliest leaves of this species were not obtained, the youngest found being in the *Vittaria* stage. (See FIG. 23, 24.) FIGURES 20 and 21 show, however, how the *Polytaenium* type of venation may be developed from the *Vittaria* type. As the mature venation of *Ananthacorus* is like that of *Polytaenium* and *Anetium*, it is safe to assume that these genera follow a similar course in their ontogeny.

One relationship, already briefly referred to, stands out as particularly important, i. e., the homology existing between the costal areolae in *Polytaenium* and the only areolae in *Vittaria*. (Compare FIG. 20–23 with FIG. 11, etc.) The secondary areolae in the *Polytaenium* type arise evidently by the unequal dichotomy of the veinlets forming the costal areolae, and as each of these usually divides twice, the relation between the size of the successive areolae is naturally, as already noted, approximately 1 : ½ : ¼, except as modified by divergence from the midvein.

ANTROPHYUM RETICULATUM (Schk.) Kaulf. (PLATE 8, FIG. 24–28)

Perhaps the best evidence as to the generic distinction of *Antrophyum* and *Polytaenium* is afforded by their ontogeny as figured. The earliest stages of *Antrophyum* were not obtained

but there is no reason to suppose these would differ from those already described for other species of the Vittarieae; it probably passes through a similar *Monogramma dareicarpa* stage. Very likely, too, a second *Hecistopteris*, i. e., free-veined stage occurs. But in no further stage, if *A. reticulatum* may be taken as typical, is *Antrophyum* like either *Vittaria* or *Polytaenium* (PLATE 8, FIG. 24–28).

If the ontogenetic series may be accepted as historically accurate, *Antrophyum* is derived perhaps from a form like *Hecistopteris* and is "contemporaneous" with *Vittaria*, which probably had a like origin. *Polytaenium*, on the other hand, passes through a *Vittaria* stage, and is thus not only on a line divergent from that of *Antrophyum*, but is also of a "later" generation.

It may be objected that the ontogeny of one species is slight evidence upon which to base conclusions for a genus containing upwards of twenty-five species. This is a valid objection, but it is counterbalanced in this case by the mass of supporting evidence already adduced, derived from the mature plants.

MONOGRAMMA and HECISTOPTERIS

I have no data for the ontogeny of *Monogramma* and none for *Hecistopteris*, unless perhaps some of the smaller leaves of the latter genus figured (PLATE 4, FIG. 1 and 22) represent juvenile stages. There is little likelihood, however, that these two genera pass through growth stages of a type distinct from the ordinary type seen in the other genera.

Hecistopteris probably begins, as indicated by the two figures just noted, with a uninervate *Monogramma dareicarpa* stage and proceeds then by simple dichotomy to the characteristic free-veined condition of its mature leaves. In *Monogramma* it is hardly possible that the two simplest species, *M. dareicarpa* and *M. graminea*, are ever anything but uninervate. It would be interesting to see, however, whether the larger species pass through a free-veined *Hecistopteris* stage before reaching the mature areolate condition.

IV. GENERAL CONSIDERATIONS

In the foregoing pages, I have endeavored to describe the mature sporophytes and the ontogenetic stages of the Vittarieae

without speculation as to their significance. But because of the facts presented, three questions stand out as of especial interest.

First, what are the probable relationships of the Vittarieae? Second, what is the significance of the simple type in *Monogramma*? Third, what evidence as to the theory of recapitulation is offered by the parallel venation series seen in the mature sporophytes and in the growth stages of the more advanced genera?

1. RELATIONSHIPS OF THE VITTARIEAE

Before considering the possible relationships of the tribe, it should be emphasized that only those characters in which all the genera agree, or which appear regularly in the more primitive genera, may be used for comparison. This fact may seem too self-evident to need stating, but its disregard has led to some erroneous comparisons, of which I have contributed one in comparing *Antrophyum* with *Loxogramma* Presl of the tribe Polypodieae.*

The characters in which all the genera agree are found in the arrangement of the sporangia, in the type of rootstock scales, and in the presence of the differentiated epidermal idioblasts. Goebel found that the prothallia of a number of species in *Vittaria*, *Hecistopteris*, and *Monogramma* are of a peculiar type characteristic of the tribe. E. G. Britton and A. Taylor added *Vittaria lineata* to the list of species known to show the specialized type of prothallium, and I have found the same specialized sort in *Polytaenium lanceolatum* and in *Vittaria* (*Radiovittaria*) *remota*, two groups for which the gametophyte has not before been noted. Now there remains only to show that this type is characteristic also of *Antrophyum*, *Ananthacorus*, and *Anetium*, in order to demonstrate beyond a doubt that it is a tribal character. One other character may be included here as characteristic of the Vittarieae generally, viz., the uniformly parenchymatous structure in all parts except the vascular bundles.

Of these characters, the first two mentioned offer the best basis of comparison with other fern tribes, and furthermore both seem to indicate similar relationships. The resemblance in the sporangial arrangement to that which obtains in the Pteridieae

* Bull. Torrey Club **34**: 445. 19 O 1907.

is very obvious and probably justifies their juxtaposition in a systematic arrangement, as in Diel's treatment of the ferns in Engler and Prantl, Die Natürlichen Pflanzenfamilien. But there are also in the tribe Asplenieae similar and almost as obvious resemblances and it is not unlikely that here also some not very distant relationship is indicated.

The presence of clathrate scales in both the Pterideae and Asplenieae is further indication of a relationship. The use of scale characters in the classification of ferns is amply justified from taxonomic practice and experience (see Christensen, Am. Fern Journal 1: 36. 13 F 1911), and it is also justified on a priori grounds. Thus, it would seem reasonable to suppose that one type of scale may serve the purpose of protection about as well as another of the same size, and that if there are differences found, these represent not adaptive but orthogenetic tendencies. It follows that similarity in scales may usually be attributed to similarity in phylogeny.

The other three tribal characters mentioned are probably more distinctive of the Vittarieae than indicative of relationships.

As characters which appear regularly in the more primitive genera of the tribe, there may be mentioned, first, the presence of paraphyses, second, the production of the sporangia in grooves.

Both of these characters appear significant because they are all but general for the tribe; but whether they have any value in determining relationships may well be questioned, since both appear to be so definitely connected with the same function, that of protecting the developing sporangia. There is, however, strong suggestion of similar indusial developments in some of the Asplenieae, Pterideae, and Davallieae.

A character which is also of almost general occurrence in the tribe, but which cannot be considered of value in determining relationships with other tribes, is found in the reticulate venation, true for all but the three most primitive species. Ferns in general are usually believed to have sprung from primitively dichotomously veined forms and it has been shown that the present tribe is probably no exception in that respect, but the venation types above the dichotomous stage, i. e., *Vittaria*, etc., must be recognized as having been evolved independently, no matter if exactly

similar to venation patterns found in other tribes. For example, the twin net type of venation, as in *Polytaenium*, which is not uncommon in other tribes of ferns, cannot be used as a basis for comparison but must be considered as of independent origin in each tribe.

2. SIGNIFICANCE OF MONOGRAMMA

The significance of *Monogramma* is a difficult problem to solve. On the assumption of a dichotomously veined leaf as generally primitive for ferns, first stated by Goebel, I believe, *Monogramma* and the whole tribe Vittarieae might be considered as the affirmative exception to the rule. But here a difficulty presents itself, since the other genera appear usually to pass through a dichotomous stage following the uninervate beginning. The uninervate type must then either be recognized as more primitive than the dichotomous type or else as a derived condition in this tribe. Study of the first leaves of other simple-leaved ferns is needed.

The marginal position of the sporangia in *M. dareicarpa* and *M. graminea* is in agreement with Bower's suggestion as to the probable primitive condition for ferns. It is interesting to note here that the attainment of the dorsal position in the other genera is a direct consequence of the branching of the veins, since all or any of the veins appear to be potentially sporangiferous. Bower assumes, however, a primitively divided type with only marginal or submarginal sori, the dorsal position having been attained by the migration of the sori. In this hypothetical primitive type the sporangia are assumed to have been definitely localized in sori, not as in the present case in lines of indeterminate length. The present tribe is interesting in this respect because it offers an instance of the development of an approach to a soral condition (as in *Anetium*) from an indeterminate development of lines of sporangia.

But whatever the phylogenetic significance of *Monogramma*, its position, at least as regards two of its species, as the simplest of known vascular plants can scarcely be questioned. The leaf structure is analogous in its simplicity to that of the lycopods generally. The stele, it may be noted, as far as I have been able to determine from sections of soaked herbarium material, is a very

simple protostele in three of the species, *M. dareicarpa*, *M. subfalcata*, and *M. trichoidea*. In these the xylem strand is only a few cells thick. In *M. paradoxa* the stele is a simple siphonostele with a tiny ring of xylem and with the phloem apparently only outside.

Monogramma may well be considered as the "*Amphioxus*" type for vascular plants, and as such deserves thorough study and a place in any future course in the comparative morphology of vascular plants.

3. EVIDENCES OF RECAPITULATION IN THE VITTARIEAE

In a paper entitled "Juvenile kelps and the recapitulation theory,"* R. F. Griggs has drawn attention to the fact that botanists have generally accepted and applied the theory of recapitulation to interpret plant phylogeny without attempting to test its truth. Griggs directed attention also to the objections that have been raised against the theory by several zoologists. In his study of the kelps, he reached the conclusion that these objections are not well founded and that there is shown by these plants distinct evidence of recapitulation. I wish here to consider briefly the case of the parallel venation series furnished by the Vittarieae, in order further to test the application of the recapitulation theory.

Most of the objections appear to be built around the assumption that, since whenever a new species is produced its germ cells must contain the means of reproducing the new character, the whole ontogenetic history of a new form is on this account necessarily different from that of the parent form. Those who accept this assumption explain parallel series as due to necessity, that is, the organism in its growth repeats stages like the adult forms of its ancestors because such stages are structurally or physiologically necessary. According to this objection it should be necessary only to show that in some cases the ontogeny repeats stages that are not necessary to the attainment of the later form.

Griggs described stages in the growth of certain of the kelps, to which the argument of necessity would not seem to apply. Numerous such examples have been noted in the animal kingdom and there appears to be another well-defined example of a similar

*Am. Nat. **43**: 5–30; 92–106. 1909.

inheritance of an unnecessary juvenile character in some of the ferns treated here.

There is no evidence of the repetition of an unnecessary character in the development of the twin net type of venation from that of *Vittaria*. It is impossible in this group to conceive of the higher type being developed from the simpler in any way but by the addition of secondary areolae along the previously formed costal areolae of the *Vittaria* stage. Similarly there is no evidence in the series found in *Vittaria remota* to show that any unnecessary stages were passed through here.

But when the ontogeny of *Vittaria remota* is compared with that of *V. intramarginalis* a striking difference is to be noted. Both finally reach the same venation type, the only difference being that *V. remota* carries this type to a greater specialization than is found in the other *Vittaria*. In its ontogeny, however, *V. intramarginalis* passes through a free-veined stage like the mature condition of *Hecistopteris*, a stage which, as compared with the course of growth in *V. remota*, can hardly be considered otherwise than unnecessary.

It has already been noted that *Vittaria intramarginalis* is to be considered lower in the evolutionary scale than *V. remota*, and this conclusion accords exactly with the differences in the ontogeny. Naturally the more primitive species would longer retain unnecessary ancestral characters.

SUMMARY

Several conclusions from the above study seem to deserve the emphasis of a repetition in the summary.

1. The Vittarieae represent a well-defined, rather specialized natural group of ferns probably related to the Pterideae and to the Asplenieae. Seven genera are to be recognized, *Monogramma* Schk., *Hecistopteris* J. Sm., *Vittaria* J. E. Sm., *Polytaenium* Desv., *Ananthacorus* Und. & Maxon, *Anetium* Splitg., and *Antrophyum* Kaulf.

2. The genus *Monogramma* includes two species, *M. dareicarpa* Hook. and *M. graminea* (Poir.) Schk., which seem to possess the simplest leaf and stem structure known among vascular plants.

3. The seven genera may be arranged according to their vena-

tion patterns in a phylogenetic series beginning with *Monogramma* and ending doubly, with *Anetium* on the one hand, and with *Antrophyum* on the other.

4. The more advanced genera show in their ontogeny successive venation stages similar to those noted in the phylogenetic series.

5. The species whose ontogenies were studied differ from most ferns in beginning with a uninervate type, but usually they show secondarily the free dichotomous venation found in other ferns.

6. The tribe illustrates clearly how one type of areolate venation may have been derived from a free dichotomous type.

7. In comparing the parallel adult and ontogenetic venation series, affirmative evidence for the theory of recapitulation is found in the inheritance in at least one primitive species of *Vittaria* of an unnecessary juvenile stage which in another more advanced species of *Vittaria* has been eliminated.

COLUMBIA UNIVERSITY.

Explanation of plates 2-8

PLATE 2. Illustrating tribal characters

FIG. 1. *Anetium citrifolium;* portion of leaf, natural size, showing venation and arrangement of sporangia; from *von Tuerckheim 9625*, Guatemala.

FIG. 2, 3. *Ananthacorus angustifolius;* 2, cross-section of leaf, × 12, showing sporangial grooves; 3, portion of leaf, natural size, showing venation and arrangement of sporangia; both *Underwood & Earle 1175*, Cuba.

FIG. 4, 5. *Vittaria minima;* leaves, natural size, to show venation and arrangement of sporangia; 4, *Werckle*, Costa Rica (type material of *Hecistopteris Werckleana* Christ); 5, *Enares*, Costa Rica (type material of *Antrophyum minimum* Baker).

FIG. 6. *Antrophyum nanum;* single plant, natural size, showing venation and arrangement of sporangia; from *R. S. Williams 2826*, Philippines.

FIG. 7, 8. *Monogramma paradoxa;* a, spicular cells (after Luerssen).

FIG. 9, 10. *Vittaria stipitata;* rhizome scales; 9, *H. H. Smith 1112*, Santa Marta, Colombia; 10, *Werckle*, Costa Rica.

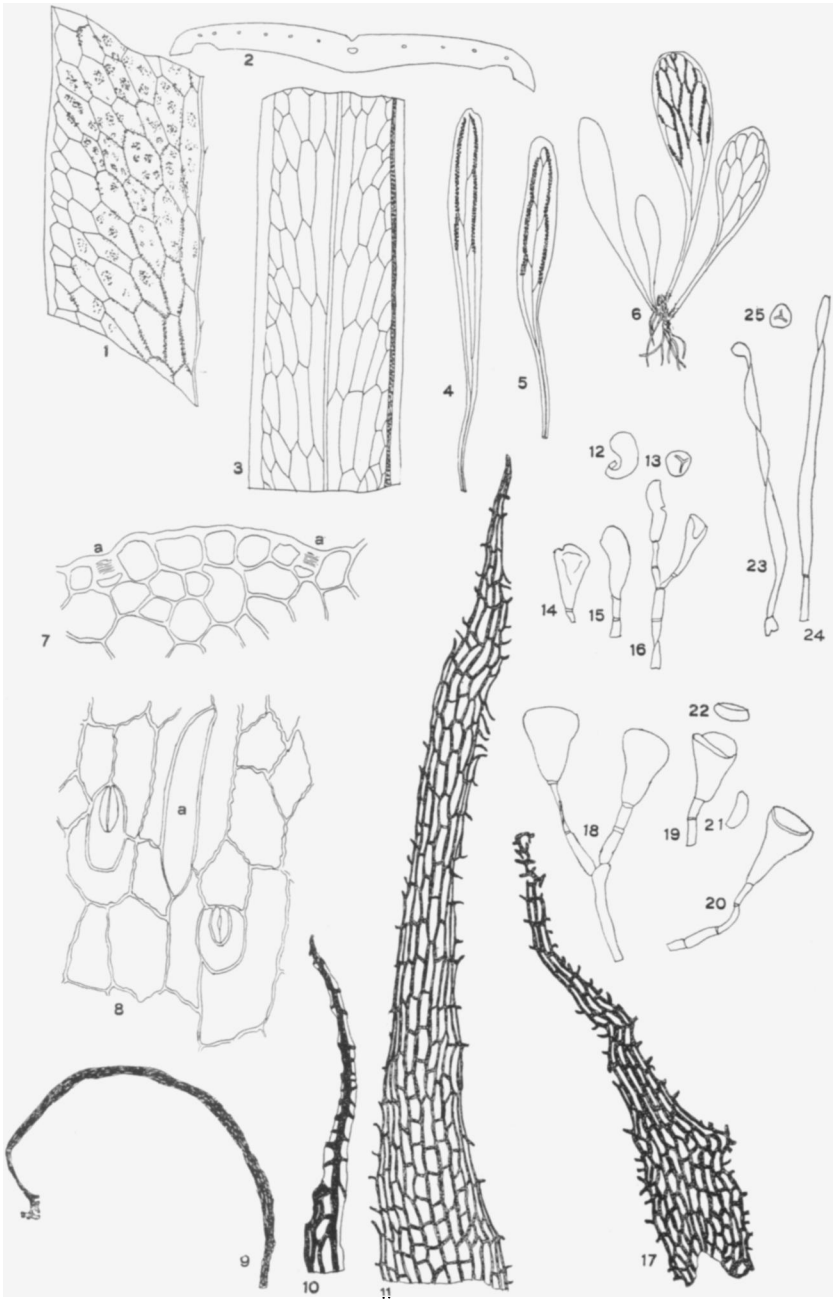
FIG. 11–16. *Vittaria scabrida* (?); *W. R. Maxon 3313*, Guatemala; 11, rhizome scale, × ca. 75; 13, spore much enlarged; 12, 14–16, paraphyses, much enlarged.

FIG. 17–22. *Vittaria remota; R. S. Williams 889*, Panama; 17, rhizome scale, × ca. 75; 18–20, paraphyses, much enlarged; 21, 22, spores.

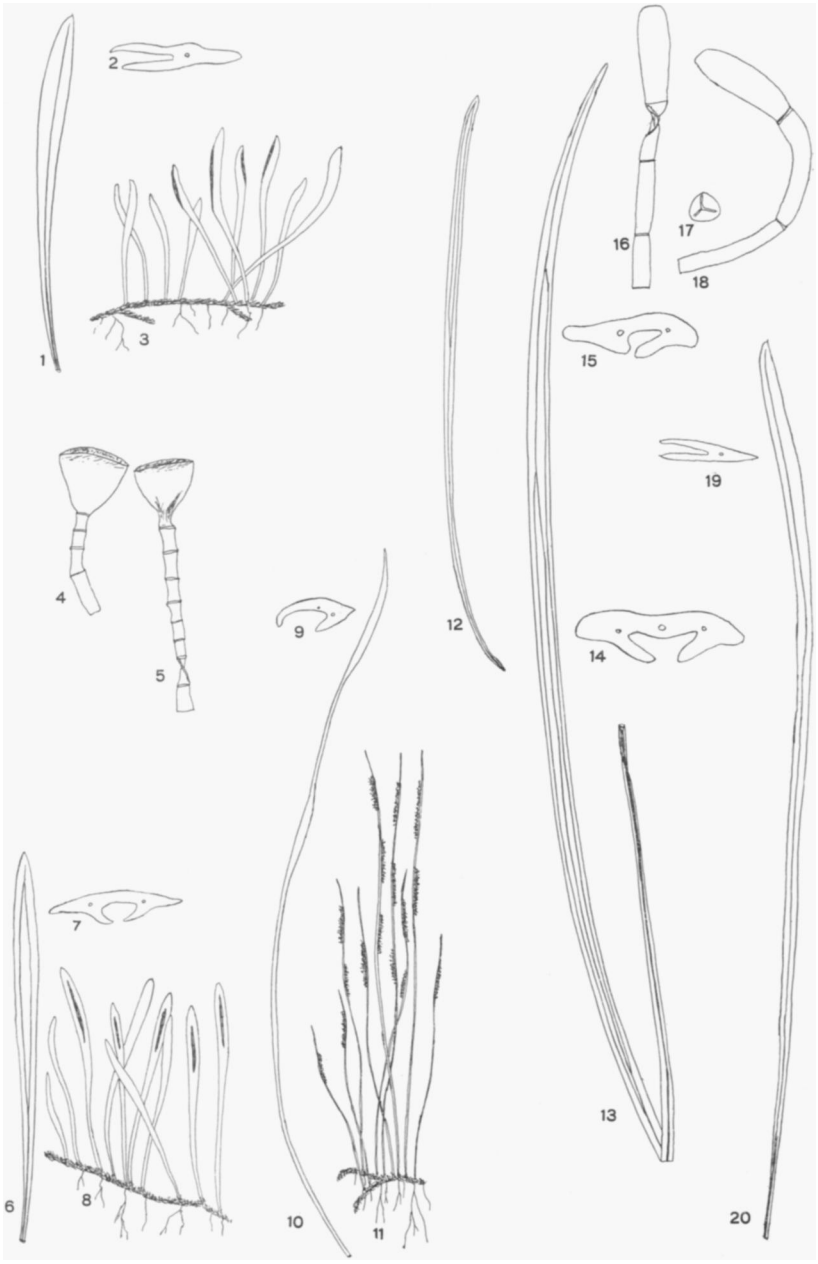
FIG. 23–25. *Antrophyum semicostatum, R. S. Williams 2054*, Philippines; 23-24, paraphyses, much enlarged; 25, spore, much enlarged.

PLATE 3. *Monogramma*

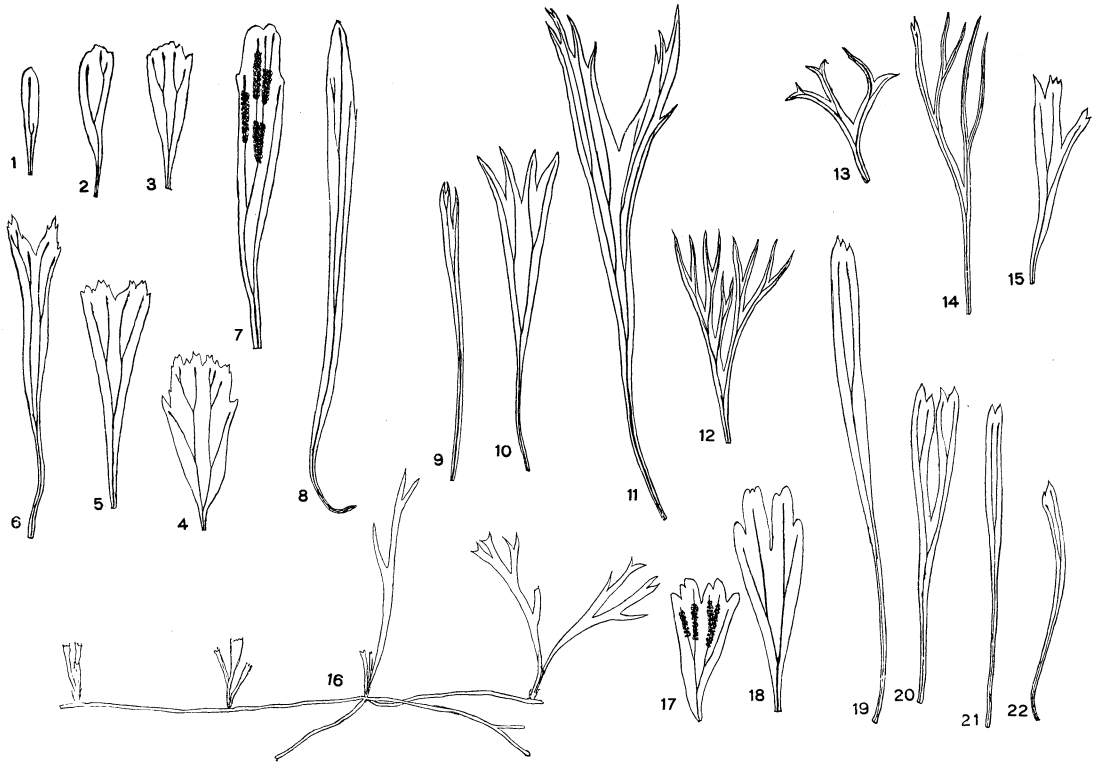
FIG. 1–3. *M. dareicarpa; E. B. Copeland 63*, Negros, Philippines; 1, leaf showing venation, × 2; 2, cross-section of leaf to show sporangial groove, × 12; 3, whole plant, natural size.



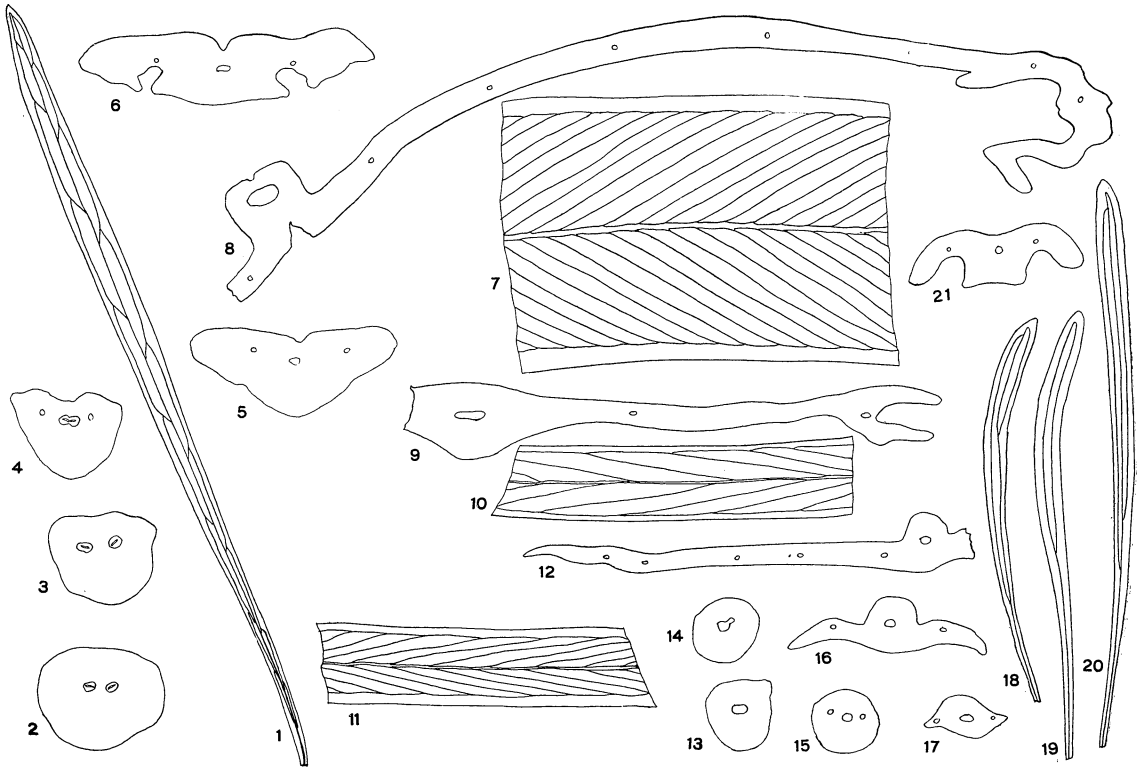
BENEDICT: VITTARIEAE, TRIBAL CHARACTERS



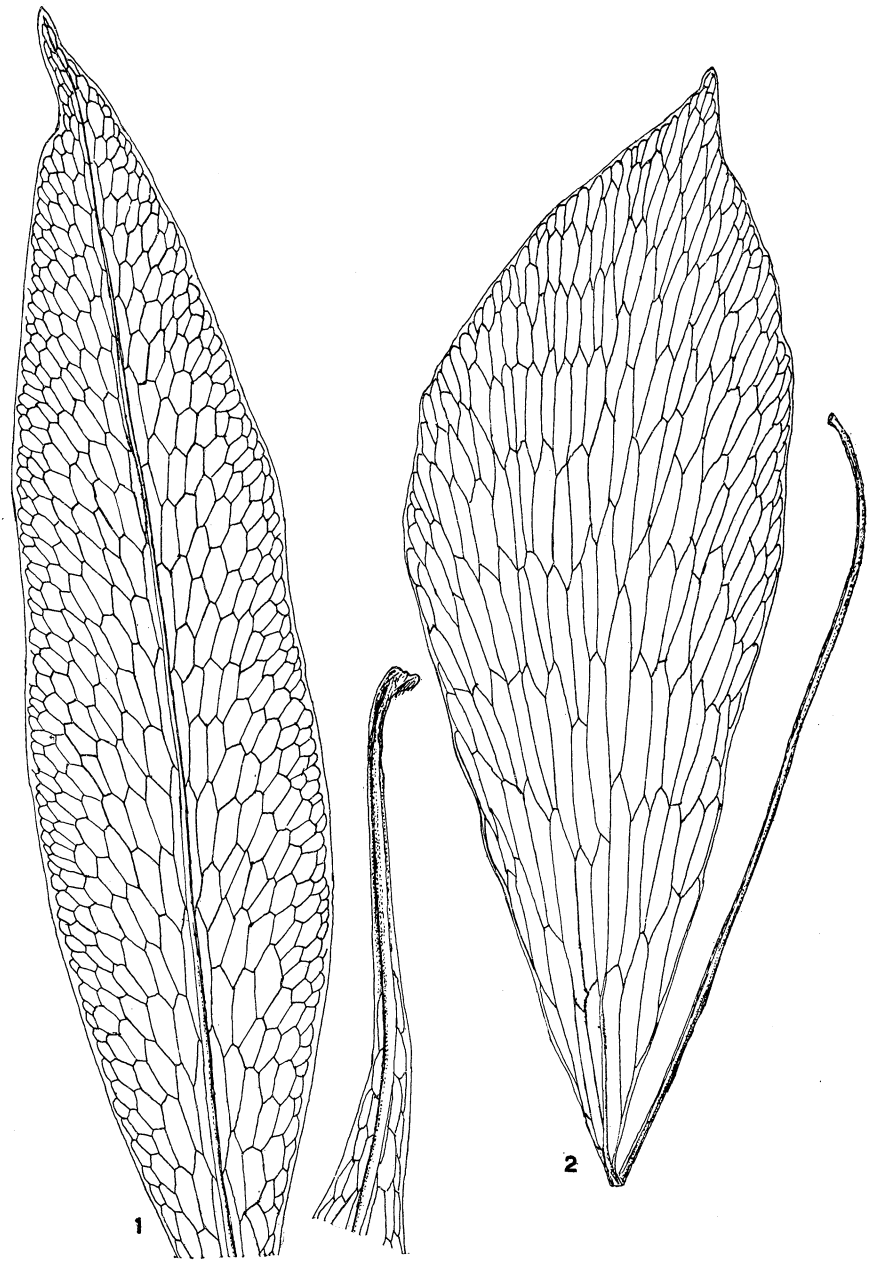
BENEDICT: VITTARIEAE, MONOGRAMMA



BENEDICT: VITTARIEAE, HECISTOPTERIS



BENEDICT: VITTARIEAE, VITTARIA



BENEDICT: VITTARIEAE, POLYTAENIUM and ANTROPHYUM

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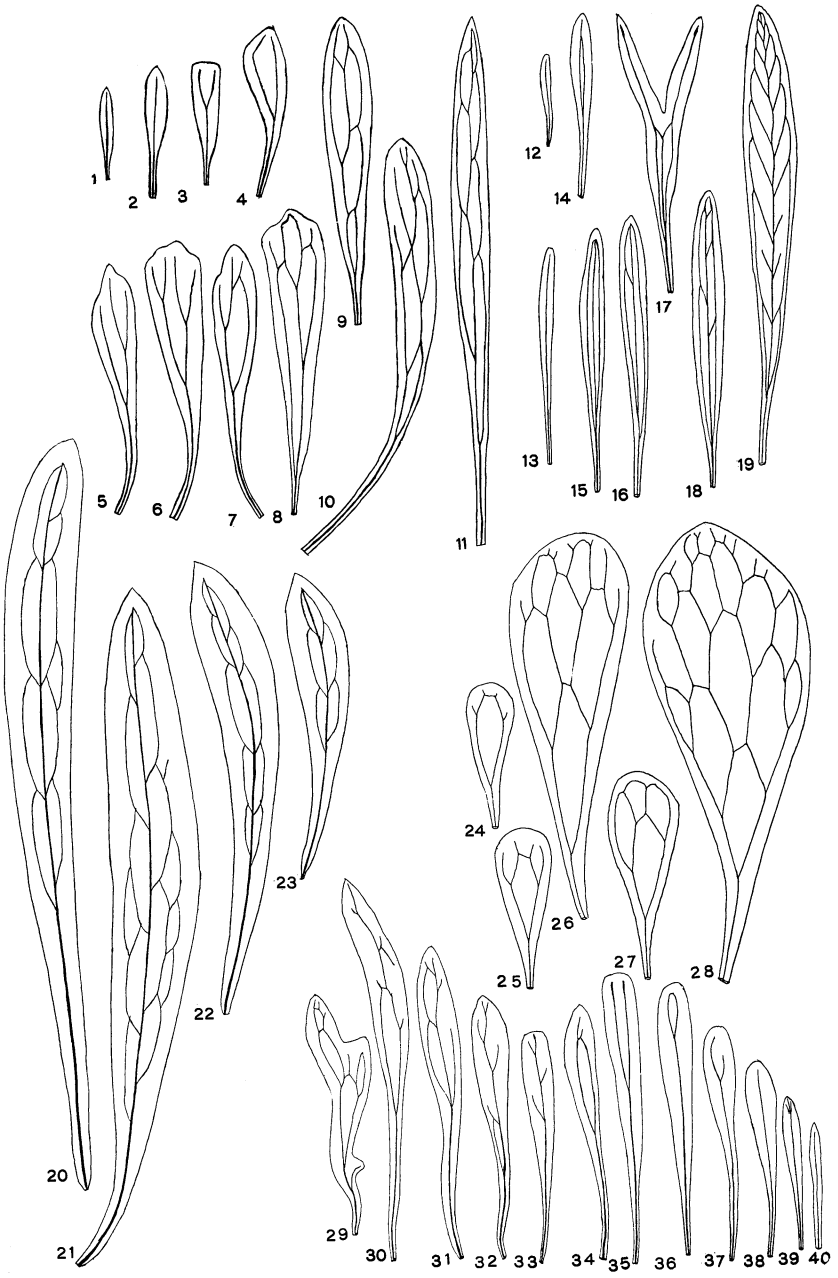

BENEDICT: VITTARIEAE, ONTOGENETIC STAGES

FIG. 4, 5. Paraphyses of the *M. graminea* type, much enlarged.

FIG. 6–8. *M. subfalcata;* after Hooker, Sp. Fil. **5**: 122. *pl. 289 a.* 1864, showing venation; 6, section of leaf; 7, habit of plant; 8, enlargement as in *M. dareicarpa.*

FIG. 9–11. *M. trichoidea;* illustrating same features as preceding species; enlargements the same; 9, *E. B. Copeland 1723,* Mindanao; 10, 11, *R. S. Williams 2230.*

FIG. 12–15. *M. paradoxa;* showing venation (12 and 13) and leaf sections (14 and 15), the sections having been taken at about the positions indicated on FIG. 13; 12, *R. S. Williams 1492,* Luzon; 13–15, *Bolles,* Samoa.

FIG. 16–18. Paraphyses (16 and 18) and spore (17) of *M. paradoxa.*

FIG. 19, 20. *M. graminea;* showing venation and leaf section; enlargement as in similar figure preceding.

PLATE 4. *Hecistopteris*

FIG. 1–22. Showing leaf outlines, venation, and arrangement of sporangia (7 and 17); sporangia present but not indicated on most of the other leaves; enlargement in all cases × 2. 1–8, *R. S. Williams 1159,* Bolivia; 9–12, *Jenman,* Kara Kara Creek, British Guiana; 13–15, *Jenman,* Essequibo River, British Guiana; 16–18, *Jenman,* Trinidad; 19–22, *R. S. Williams 1172,* Bolivia.

PLATE 5. *Vittaria*

FIG. 1–6. *V. intramarginalis; Underwood & Earle 875,* Cuba; 1, leaf, showing venation, ×2; 2–5, cross-sections of petiole showing double leaf trace at base (2, 3) and its fusion to form single midvein (4, 5); 6, cross-section of lamina at about the middle to show sporangial grooves; all sections enlarged 12 times.

FIG. 7, 8. *V. scolopendrina;* 7, *E. D. Merrill 5861,* Mindoro; 8, *Bolster 308,* Mindanao; 7, portion of leaf, × 2, showing venation; 8, cross-section from midvein to margin, ×12, showing sporangial groove.

FIG. 9, 10. *V. "elongata"; Copeland 1516,* Mindanao; 9, cross-section of leaf, ×12, showing sporangial groove; 10, portion of leaf, ×2, showing venation.

FIG. 11–17. *V. remota; R. S. Williams 889,* Panama; 11, portion of leaf, ×2, showing venation; 12, cross-section of leaf blade, ×12, showing very slight sporangial groove; 13–17, cross-sections of petiole from base to beginning of blade, ×12, showing a single leaf trace.

FIG. 18–21. *V. sikkimensis, A. Henry 10489,* Szemao, China; 18–20, leaves, × 2, showing venation like that of large *Monogramma paradoxa* (PLATE 2); 21, cross-section of leaf × 12, showing two separate sporangial grooves characteristic of *Vittaria.*

PLATE 6. *Polytaenium* and *Antrophyum*

FIG. 1. *Polytaenium cayennense; Fendler 151,* Trinidad; leaf slightly reduced in size, showing twin net type of reticulate venation.

FIG. 2. *Antrophyum plantagineum; R. S. Williams 2444,* Mindanao; leaf slightly reduced in size, showing single net type of reticulate venation.

PLATE 7. *Polytaenium* and *Antrophyum.*

FIG. 1, 2. *Antrophyum stenophyllum; A. Henry 9607,* Szemao, China (type number, first time illustrated); 1, whole plant, ×½, showing arrangement of sporangia; 2, leaf, ×½, showing venation.

FIG. 3–5. *Polytaenium lanceolatum* var. *Feei;* Mexico; 3, *H. Fink 115;* 4 and 5, *F. Müller;* leaves ×½, showing venation and arrangement of sporangia.

FIG. 6. *Polytaenium discoideum; R. S. Williams 1355*, Bolivia; leaf, ×½, showing venation and arrangement of sporangia.

FIG. 7. *Antrophyum Williamsi* Benedict (see Am. Fern Jour. 1: 70. 1911); *R. S. Williams 1579*, Luzon; plant, ×½, showing arrangement of sporangia in lines, as in middle leaf, and their apparent confluence at maturity.

FIG. 8–10. *Polytaenium quadriseriatum* Benedict; *Nash & Taylor 1360*, Hayti, type; 8, leaf, natural size, showing venation and arrangement of sporangia; 9, 10, cross-sections of leaves, ×12, showing sporangial grooves.

PLATE 8. Ontogenetic stages

(All figures except 19 twice natural size)

FIG. 1–11. *Vittaria intramarginalis; Underwood & Earle 875*, Cuba.

FIG. 12–19. *Vittaria remota;* from plants grown at the N. Y. Botanical Garden, spores from Jamaica; 19, natural size.

FIG. 20–23. *Ananthacorus; Underwood 2767*, Jamaica.

FIG. 24–28. *Antrophyum reticulatum; C. B. Robinson*, Bureau of Science, *9915*, Luzon.

FIG. 29–40. *Polytaenium lanceolatum ;* from plants grown at the N. Y. Botanical Garden, spores from Cuba (*Taylor*).